



Research Paper

Assessment of canola crop lodging under elevated temperatures for adaptation to climate change

Wei Wu^{a,b}, Bao-Luo Ma^{b,*}^a College of Agronomy, Northwest A & F University, Yangling 712100, Shaanxi, China^b Ottawa Research and Development Centre, Agriculture and Agri-Food Canada, 960 Carling Ave, Ottawa, ON, K1A 0C6, Canada

ARTICLE INFO

Keywords:

Global warming
High temperature stress
Brassica napus L.
Crop lodging
Anchorage failure

ABSTRACT

With temperatures rising due to global climate change, many endeavors have been looking into how this will affect crop production and food security. Lodging, which is the permanent displacement of crop plants from upright position, is one of the main causes of yield loss and quality reduction in canola/oilseed rape. However, there has been little research to date on how the mechanisms of crop lodging might be affected by high temperature. The objectives of this study were to examine the effect of high temperature on the structural features of lodging resistance in four canola genotypes, to determine what kind of lodging (stem or root) was more prevalent, and to identify corresponding mechanistic traits associated with lodging under high temperature conditions. The experiment was carried out in controlled growth facilities with the genotypes tested under normal (23/17 °C; CK) and high temperature (27.01/24.3 °C) regimes. The results showed that high temperature reduced root lodging resistance significantly, as indicated by a dramatic reduction in both root anchorage and safety factor (against anchorage failure). These were attributable to the large suppression on lateral root growth (32%), and thereby reduction in root bending resistance (33%), root–soil cone dimension (13%), and its shear strength (33%). High temperature showed an inconsistent effect on stem lodging resistance, which was in alignment with the engineering mechanics theory and supported by the anatomical observations. These results indicated that canola genotypes were more prone to anchorage failure than stem buckling. Consequently, root lodging resulted from anchorage failure would become a critical aspect under rising temperatures with the global warming. The present study indicates that root lodging should be targeted as a priority to improve crop lodging resistance through breeding selection for a root system with high anchorage strength, especially when the crop plants are expected to encounter inevitable high temperature stress.

1. Introduction

World food security and agricultural production are directly affected by global warming (Peng et al., 2004; IPCC, 2007; Battisti and Rosamond, 2009; Lobell et al., 2011; Singh et al., 2013). Therefore, extensive research has been conducted to project the potential impacts of global warming on agricultural productivity through *in situ* experimentation, and using crop and global climate models (Tao and Zhang, 2011; Ma et al., 2010). Canola (*Brassica napus* L.) is one of the world's most important oilseed crops and the most profitable commodity for Canadian farmers (Canola Council of Canada, <http://www.canolacouncil.org/oil-and-meal/what-is-canola/>). As a C₃ cool season crop, canola is more susceptible to heat stress than other C₃ and C₄ field crops. High temperatures significantly change the rate of plant metabolic processes that ultimately reduces biomass accumulation, and grain formation (Tripathi et al., 2016). For example, in a field study

conducted in eastern Canada, both harvest index and seed yield were reduced by as much as 40% in 2012, a year with severe heat and drought stress, compared to a year with more or less normal temperatures (Ma and Herath, 2016).

Lodging, the permanent displacement of aboveground portions of the crop from the upright position is caused by the interactions between the biophysical properties of the plant and environmental forces such as wind, storm, rain, or hail. Lodging is a common phenomenon in canola production and the main constraint for increasing canola yields under excessive nitrogen application and favorable weather conditions (Pinthus, 1973; Goodman et al., 2001; Foulkes et al., 2011). Multiple studies on grain cereal crops, such as rice, wheat, barley and oat have shown that lodging can decrease both yields and grain quality (Pinthus, 1973; Ma et al., 2012). Lodging can also cause problems for harvest operations and consequently, production costs (Berry et al., 2004). Hence, scientific understanding of high temperature impact on crop

* Corresponding author.

E-mail addresses: baoluo.ma@agr.gc.ca, Wei.Wu@agr.gc.ca (B.-L. Ma).

lodging is of critical importance in crop adaptation to future global climate change.

Crop lodging can be classified as stem lodging and root lodging (Berry et al., 2003a; Wu and Ma, 2016). Stem lodging is mainly due to previous tissue damage by insects and diseases or physically by storm and hail that break the basal internodes of the stem (Pinthus, 1973). Stem lodging resistance is related to the morphological and mechanical characteristics of basal internodes, such as stem diameter, bending strength, flexural rigidity and Young's modulus, etc. (Berry et al., 2004). Root lodging is induced by the failure of the root–soil anchorage system (Ennos, 2004). Root lodging risk depends on the external force exerted on the self-weight moment (bending moment) of the intact plant and anchorage strength of the root system. Crook and Ennos (1993, 1994) suggested that root lodging should be regarded as predominant over stem lodging in modern wheat cultivars. Baker et al. (1998) and Berry et al. (2003a) further reasoned that both types of lodging were possible depending on the circumstances of a particular crop. For example, moist and sandy soils increased the risk of root lodging over that of stem lodging due to weakened soil shear strength (Sposaro et al., 2008). Application of high nitrogen rate, and high plant population densities, both can increase the risk of stem lodging over root lodging due to weakened stem bending strength and extended plant height (Pinthus, 1973; Wu et al., 2012). The underlying properties that cause the stem and root lodging should be differentiated (van Delden et al., 2010; Wu and Ma, 2016). Classifying the root and stem lodging susceptibility of genotypes under specific environment is of importance to decision-making on choosing the appropriate strategies for minimizing the most likely form of lodging.

To effectively adapt to future climate changes, several strategies, such as breeding selection, agronomic practice and crop rotation have been undertaken to mitigate its negative impact on canola yield performance. High or warmer temperatures have been shown to induce the floral sterility or pollen abortion, and shorten seed filling duration and subsequently reduce inflorescence size in canola plants (Morrisson and Stewart, 2000; Shah et al., 2011). It may result in less self-weight moment, potentially compromising stem lodging resistance. Furthermore, high and warmer temperatures could alter the partitioning of photoassimilate to roots, and suppress root growth/extension or change root system architecture (Tripathi et al., 2016), or even decrease the elliptical root–soil cone volume. Therefore, root anchorage strength is reduced. High or warmer temperatures would also accelerate cell growth and cell proliferation, which may lead to larger cells with thinner cell walls and weakened vascular bundles that would negatively influence the Young's modulus of plant tissues (Trueba et al., 1982; Ristic and Cass, 1991). In a field study, late-seeded canola plants often produced a smaller root system, due to higher temperature and/or drought stress encountered during the crop development, and was therefore more prone to root lodging than the optimum-seeded canola plants (Wu and Ma, 2016).

Although it is known that high temperatures could affect the morphological and agronomic characteristics of shoot and root, few published studies have considered the direct impact of high temperatures on root and stem lodging resistance, and on the variations in related structural features. To date, only one study (Zhu et al., 2013) suggested that elevated soil temperature alone or together with CO₂ enrichment increased the risk of stem lodging in rice plants. Unfortunately root lodging risk was not examined in their study. Furthermore, there were no studies examining the prevalence or susceptibility between stem lodging and root lodging of canola plants subjected to high temperature environments. High temperature stress has recently been reported to alter biomass production (Ma and Herath, 2016), nutrient uptake, distribution and balance (Ma and Zheng, 2016). Thus, we hypothesized that (1) high temperature stress would significantly influence lodging resistance, and (2) high temperature may exert a different force on stem and root lodging susceptibility. A better understanding of those mechanisms will be helpful to mitigate the most likely form of lodging. The

objectives of this study were to (1) assess the impact of high temperature stress on stem and root lodging resistance in four different genotypes under controlled growth facility conditions, (2) determine which kind of lodging (stem or root) is more susceptible under high temperature stress, and (3) identify lodging-related morphological, biophysical, mechanical properties. This knowledge will be useful to plant breeders, and/or agronomists for canola improvement, and/or selection of genotypes of canola that is more resistant to lodging under increased temperature with global warming.

2. Materials and methods

2.1. Plant and treatments establishment

A pot culture experiment was conducted in a controlled environment at the Ottawa Research and Development Centre Laboratory of Agriculture and Agri-Food Canada, Ottawa, ON, Canada. Treatments were arranged in a split-plot design with temperature treatment as the main-plot and genotype as the subplot, to form a randomized complete block design. Four canola genotypes were tested in this study. Two genotypes (13C220 and 13C204) were kindly provided by Dr. Rob Duncan from the University of Manitoba, Winnipeg, Canada, and the other two were commercial hybrids (Pioneer45A65 and Invigor5440). Invigor5440 shows strong lodging resistance and is commonly used as a check cultivar in provincial canola cooperative performance trials conducted in Ontario and Quebec. These four genotypes were chosen to represent a wide range of sensitivity to lodging. Three seeds were sown in each of the 32 plastic pots (10.5 cm diameter and 9 cm height), filled with soil mix (sieved top sandy loam soil + vermiculite + peat moss + perlite). The soil mix contained 17.3 g kg⁻¹ organic C, 45 mg kg⁻¹ Olsen P, 400 mg kg⁻¹ soil test K, 4000 mg kg⁻¹ available Ca, 36 mg kg⁻¹ available Mg, 3 mg kg⁻¹ available Na, with 250 meq kg⁻¹ total cation exchange capacity, and a pH 6.6. The experiment was conducted twice in duplicate runs.

In each run of the experiment, sixteen pots were moved to each of the two growth chambers (Model GR 96, CONVIRON, Control Environment Ltd., Winnipeg, MB) for seed germination. The usable area for each growth chamber is 1.8 m² (0.9 × 2.0 m) and the distance between each pot was set at 25 cm apart. The position of the pots within each chamber was rotated at random on a weekly basis to avoid any potential light/temperature/water gradient within the chamber on plant growth. There were four replications for each genotype. The seedlings were thinned to one per pot on the 6th day after planting. The plants were grown in two growth chambers for two weeks at 23/17 °C (day/night) prior to the application of temperature treatments. Based on the long-term mean temperature and diurnal high temperature fluctuations in the summer that occur commonly in this region (Wu et al., 2017), the high temperature treatment of one growth chamber was set in a 24-h cycle as follows: 6:00–10:00 = 23 °C, 10:01–11:00 = 26 °C, 11:01–12:00 = 29 °C, 12:01–16:00 = 32 °C, 16:01–17:00 = 29 °C, 17:01–18:00 = 26 °C, 18:01–22:00 = 23 °C, 22:01–2:00 = 26 °C, 2:01–5:59 = 23 °C; and the normal temperature chamber (control) was maintained at 23/17 °C (light/dark) until maturity stage. The average temperatures in the hot and control chambers were 27.01/24.33 °C and 23.0/17.0 °C (light/dark), respectively. The growth chambers were set at 16/8-h light/dark cycle, with approximately 500 μmol m⁻² s⁻¹ photosynthetic photon flux density (PPFD) at the canopy level and 75% relative humidity. Each pot was well-irrigated to avoid any drought stress, and received 0.1 g of compound fertilizer (N: P₂O₅: K₂O = 15:15:15) once a week until 10 days after flowering stage.

2.2. Sampling and data collection

2.2.1. Simulated root lodging test

The lodging-related traits were determined for each plant at the

physiological maturity stage of canola (BBCH 89). Firstly, plants were cut off at a height of 20 cm. Simulated root lodging was performed on the remaining stem base of each plant, using a custom-made lodging meter, modified at the Mechanical Engineering Workshop of Agriculture and Agri-Food Canada (ORDC, Ottawa, ON). The meter originated from a sensitive Mecmesin digital torque screwdriver (Mecmesin, Slinfold, UK; reading up to 1.5 Nm in 0.0001 Nm intervals), according to van Delden et al. (2010). The arm of the torque screwdriver was attached to the remaining basal stem and the restoring anchorage strength (S_r) supplied by the total root system was recorded when the basal stem was pushed to a 30° angle from the vertical position. The rotation speed was approximately 2.0° S⁻¹.

2.2.2. Simulated stem lodging test

After the S_r measurements, each plant without the basal stem was balanced on a thin, smooth metal tube, and the distances between the balance point and the base end were recorded as the centers of gravity of the stem (h_s). The basal stem was cut at the ground level, and was combined with its corresponding above-ground plant as a whole by using transparent tape, and then the centers of gravity of the entire plant was recorded as h_r . In this study, we only considered the self-weight of the tissue for determining both stem lodging and root lodging, which is why the basal stem is not considered in stem lodging, but is considered in root lodging. The plant height, defined as the distance between the soil surface and the top of the plants, was measured. The fresh weight of these basal stem segments and the above plant parts were recorded immediately to avoid any weight loss. The basal stem segments were packed in plastic bags and brought to the laboratory. Stem breaking resistance was then determined by using the three-point bending test, with a stand (Multitest 2.5-I fitted with a 100 N load cell, Mecmesin, Slinfold, UK). The center of the basal stem, where the breaking resistance was measured, was aligned horizontally with the middle point between the two fulcras with a length (L) of 10 cm. The crosshead was then moved and attached to the center point of the basal stem to bend the stem vertically at a rate of approximately 50 mm min⁻¹ until it eventually buckled. The crosshead was monitored simultaneously with the corresponding computer program (Emperor™ Force and Torque Testing Software) to produce a graph of force vs. displacement. The software calculated the maximum bending force (F_{\max}), and the initial slope of the force displacement curve (dF/dY) for each sample. Because the basal stem section can be regarded as a uniform beam, the maximum bending strength of stem (S_s , Nm) was calculated as $S_s = F_{\max} \times L/4$ (Goodman et al., 2001). The diameters of the minor and major axes in an oval cross section for the basal stem segment near the breaking position were measured using a digital caliper (General Tools, NY, USA). The dry weight of the basal stem segment was measured after oven drying at 80 °C until a constant weight was achieved and then dry weight per unit length was calculated. In this study, the mechanical bending test was performed only on the basal region of the stem, although stem buckling could occur at any point of the canola stems (Baker et al., 2014). This is because the stem is generally known to crack at the basal internode stem, where it sustains the greatest self-weight moment (bending moment). In addition, it is well-documented that the strength of the plant's base was the most critical point for stem buckling in rice and barley crops (Berry et al., 2004).

2.2.3. Calculations of safety factor and mechanical properties

The safety factor (SF) represents the number of times a support organ (such as stem and root) can bear the self-weight moment (M) of the organ that it is supporting. This measure was introduced by Crook et al. (1994) to identify lodging susceptibility. The SF values against stem buckling (stem lodging, SF_s) and against anchorage failure (root lodging, SF_r) are given as follows:

$$SF_s = S_s/M_s \quad (1)$$

$$SF_r = S_r/M_r \quad (2)$$

where S_s and S_r are the stem bending strength (Nm) and root anchorage strength (Nm), as described above. The parameters M_s and M_r are the self-weight moments (Nm) at θ° from the vertical stand for the stem and entire plant and are calculated as follows:

$$M_s = \sin\theta \times h_s \times m_s \times g \quad (3)$$

$$M_r = \sin\theta \times h_r \times m_r \times g \quad (4)$$

where θ is inclination angle from the vertical stand and h_s and h_r are the heights (cm) of the centers of gravity of the stem and entire plant, respectively. In addition, m_s and m_r are the fresh weight (g) of the stem (except for basal 10 cm segment) and entire plant, respectively, and g is the acceleration due to gravity (N kg⁻¹).

Flexural rigidity (EI , Nm²), which represents the stiffness of the basal stem section, is calculated as:

$$EI = L^3 (dF/dY)/48 \quad (5)$$

Young's modulus (E , Nm⁻²), which represents the material elasticity, is calculated as:

$$E = EI/I \quad (6)$$

I is the second moment of area (m⁴), which represents the geometrical property of the basal internode that reflects how its points are distributed with regard to an arbitrary axis. It is calculated as follows:

$$I = \pi \times a^3 \times b/4 \quad (7)$$

where “ a ” is the outer diameter of the minor axis in an oval cross-section, and “ b ” is the outer diameter of the major axis in an oval cross-section.

Crook and Ennos (1993) developed an equation for theoretically integrating the soil shear strength and the root cone diameter, which was verified by Baker et al. (1998) and van Delden et al. (2010). The relationship is expressed as follows:

$$S_r = k \times \tau D^3 \quad (8)$$

where τ is soil shear strength (N m⁻²) that was measured using a shear vane (Vane Inspection Kit, Humboldt Mfg. Co. Illinois, USA); D is the root cone diameter (cm); and k is a dimensionless constant.

2.2.4. Root bending test and morphological traits

After removing the aboveground plants, each pot was taken to the laboratory and immersed in tap water for 3 h. Next, the root balls were thoroughly washed using a self-made root cleaning device to remove the soil. Great care was taken during washing to minimize the loss of fine roots and to ensure that the root system remained mechanically intact.

Ennos (1991) hypothesized that the total S_r mainly included two separate components, resistance of the root to bending and resistance of the root to axially movement through the soil media. This can be expressed as follows:

$$S_r = S_{r-b} + S_{r-a} \quad (9)$$

where S_{r-b} is the total root bending strength (Nm); and S_{r-a} is the root resistance to axial motion (Nm).

The second-order lateral roots and first-order lateral roots with diameter less than 1 mm (generally regarded as non-fixed structures that were not bent during artificial lodging) were separated from the taproots (Wu and Ma, 2016). Then, only the vertical taproot and first-order lateral roots that could maintain certain mechanically bending strength (generally with diameter more than 1 mm) were subjected to bending tests, according to Ennos (1991). S_{r-b} was the sum of root bending strength of all individual roots based on the following calculation after Ennos (1991),

$$S_{r-b} = \sum_{i=1}^n F_{\max,i} L_i (1 - \sin^2 \Phi_i \sin^2 \lambda_i) \quad (10)$$

Table 1

Means of plant height, gravity height, total fresh weight, averaged diameter, dry weight per internode length of basal stem and seed yield of four canola genotypes as affected by temperature treatment.

Temperature	Variety	Plant height (cm)	Gravity height (cm)	Total fresh weight (g plant ⁻¹)	Averaged diameter (mm)	Dry weight per internode length (mm cm ⁻¹)	Seed yield (g plant ⁻¹)
CK	45A65*	109.8 a	43.0 a	30.8 a	8.13 a	114 a	2.05 c
	13C220	88.1 c	38.3 b	25.3 b	7.63 a	108 a	2.81 b
	13C204	94.4 bc	40.0 ab	30.6 a	7.60 a	128 a	2.51 bc
	5440	100.1 b	40.7 ab	28.8 a	8.70 a	133 a	3.49 a
	Mean	98.1A	40.5A	28.9A	8.02A	121 B	2.71A
High temperature	45A65	103.0 a	39.6 a	31.0 b	8.12 ab	129 b	0.69 b
	13C220	98.0 a	38.8 a	31.3 b	8.09 ab	160 ab	0.79 ab
	13C204	90.5 a	35.6 a	31.7 ab	7.86 b	157 ab	1.07 ab
	5440	99.9 a	39.6 a	37.7 a	9.50 a	179 a	1.24 a
	Mean	97.9A	38.4A	32.9 B	8.39A	156A	0.95 B

Within a column in each temperature treatment, means followed by the same letter are not significantly different according to LSD (0.05) test. Lower-case and upper-case letters indicate comparisons among four genotypes and between two temperature treatments, respectively. *45A65 indicates genotype Pioneer45A65 and 5440 indicates Invigor5440. CK and high temperature treatment stand for 23.0/17.0 °C (light/dark) and 27.01/24.33 °C, respectively.

where F_{\max} is the maximum force of the root segment that can withstand before it fails; L is the length of the root segment; and ϕ and λ are the angles of inclination from different slopes.

Then S_{r-a} was estimated based on the calculation as: $S_{r-a} = S_r - S_{r-b}$.

After the root bend test, each of the intact roots was separated into two portions: taproots (including vertical root and first-order lateral roots that maintain certain mechanical strength) and lateral roots (mostly belonging to the root diameter within 1 mm). Taproots and lateral roots were placed separately in plastic bags to prevent desiccation and stored in a freezer at -20 °C before further morphological examination.

The root systems (including lateral and taproot portions) were scanned individually to determine root length, surface area and volume by using a scanner (Epson Expression 1640XL, Epson America, Inc., Long Beach, CA, USA) and a root image analyzer (Win RHIZO, Regent Instrument Inc., Quebec, Canada) (Fig. S1). To avoid any overlap of the root system and improve data precision, all root sections were separated from each other and emerged in water for scanning and analysis (Fig. S1b–c). The root–soil plate diameter was estimated indirectly based on the root skeleton drawn by the image analyzer using a root diameter class certification, according to Wu and Ma (2016). Only roots with diameters more than 1 mm were considered for the root–soil plate diameter calculations. Each individual section of the root system was dried at 70 °C for 72 h before weighing.

2.2.5. Cross section preparation and analyses

At maturity, the cross section (thick ≤ 0.5 mm) was cut manually from each basal stem with a razor. Then, selected cross sections were stained using toluidine blue (0.05%) for 10 s. This solution helps differentiate the components of the vascular bundle. The stained section was washed with deionized water until the toluidine blue was removed from the surface of the cross section. The cross section was then mounted on a glass slide with 100% glycerol and then examined and photographed using a Zeiss Axioplan 2.1 microscope with an AxioCam Digital photograph system. Because the whole cross-sectional area is large, 64 pictures were taken separately and then stitched together as one combined image (dimension approximately 10000×10000 with size of 700 MB) for each stem cross-sectional sample (Fig. S2). ZEN 2.3 software (Carl Zeiss Microscopy GmbH, Göttingen, Germany) was used to measure the specific area for the primary phloem fibres, secondary phloem, single fibre cell, xylem, pith, cortex with epidermis, cross-section, and total number of fibre cells. The phloem area was calculated as the sum of primary phloem fibres and secondary phloem. The vascular bundle area was calculated as the sum of xylem and phloem.

2.3. Data analysis

The experiment consisted of two blocks (i.e., two runs) in which two temperature treatments (control and high temperature stress) were assigned as the main plot, four genotypes were considered sub-plots to form a randomized complete block design, in a split-plot arrangement. The two-way ANOVA was conducted to determine treatment effects, using SAS (Version 9.3, SAS Institute, Cary, NC). Once a significant ($P \leq 0.05$) treatment effect was determined by the ANOVA, treatment mean comparisons with the conservative letter grouping were made at the 95% level of confidence by the Least Significant Difference (LSD) method. The Pearson simple correlations of S_s , S_r , SF_s , and SF_r with morphological, mechanical and anatomical parameters were evaluated using the CORR procedure of SAS, and the displayed maps were drawn using the R software (R Core Team, 2015). All statistical analyses were performed at the 5% level of significance. Figures were prepared using SigmaPlot (version 13.0, SYSTAT, San Jose, CA, USA).

3. Results

3.1. Morphological parameters and seed yield

The analysis of variance results for all parameters are presented in Table S1. High temperature treatment significantly increased total fresh weight and dry weight per internode length of basal stem by 13.8% and 28.9%, respectively, accompanying with increasing stem diameter; but had no consistent effect on plant height and gravity height, compared with the normal temperature (CK) treatment (Table 1). High temperature reduced seed yield significantly by 65% when averaged across the four genotypes. Most morphological parameters and seed yield showed significant differences among the four genotypes. In general, genotype Pioneer45A65 had the tallest plant height and gravity height. Genotype Invigor5440 displayed the largest values in total fresh weight, stem diameter, dry weight per length and seed yield.

3.2. Taproot and lateral root system

The ANOVA results showed that high temperatures had no significant effect on taproot biomass, length, surface area and volume, although a non-significant 13% decrease of taproot biomass was noted (Fig. S3). As expected, genotypes differed significantly in taproot volume and biomass, especially in the high temperature treatment. In general, genotype Pioneer45A65 displayed the lowest root length, surface area, and biomass of taproot, while genotype Invigor5440 had the greatest values.

High temperatures significantly reduced lateral root biomass,

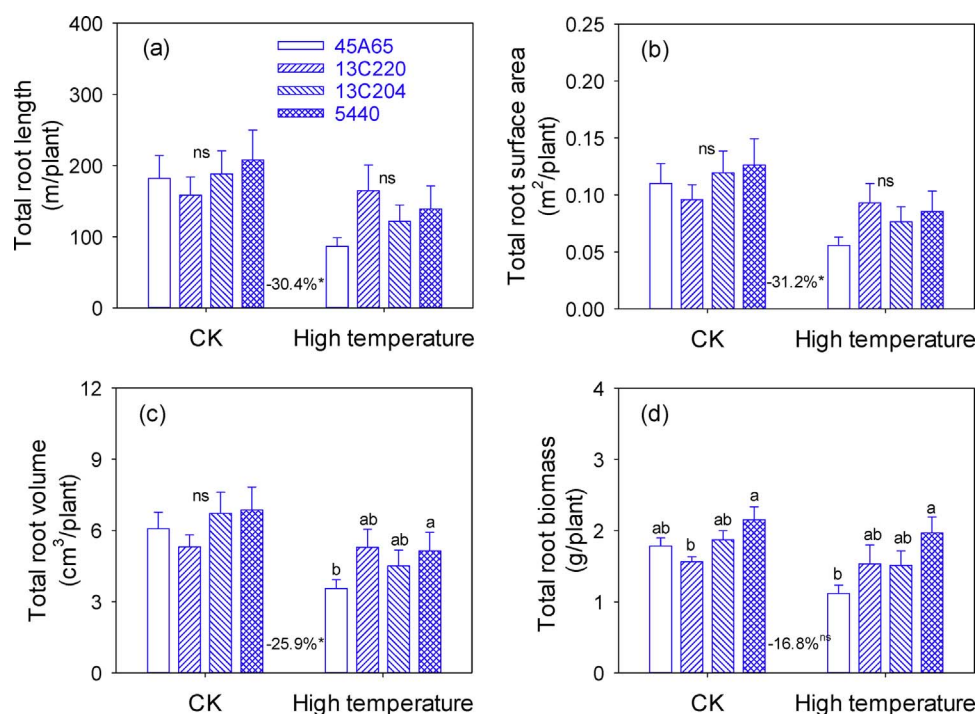


Fig. 1. Means of root length, surface area, volume and biomass of the whole root system as affected by temperature treatment and genotype. Bars of genotype means with different letters are significantly different ($p \leq 0.05$). The number between the two temperature groups is the percentage change between high temperature treatment and CK, averaged across genotypes. ns indicates not-significant ($p > 0.05$). * significant at $p \leq 0.05$. CK and high temperature treatment represent 23.0/17.0 °C (light/dark) and 27.01/24.33 °C, respectively.

length, surface area and volume by 31%–33% (Fig. S4). Genotypes exhibited large variation in these morphological traits. On average, genotype Invigor5440 displayed the highest values for these traits among the tested genotypes.

The morphological parameters of the whole root system (sum of lateral roots and vertical taproot) were all significantly reduced by high temperature, except for root biomass (Fig. 1). This was most likely due to the more dramatic effects of high temperature stress on the lateral roots rather than on the taproots. The difference in the morphological parameters of the taproots between the two temperature treatments can be negligible, as noted above.

The whole root system was classified into ten different root diameter categories (Fig. S5). It was obvious that the smallest root diameter class (0–1 mm) made greater contributions to total root volume, surface area and root length, respectively accounting for approximately 40%, 90% and 99% of the total root. There were even higher contributions of fine roots to the total under the control treatment than under the high temperature conditions, because lateral roots (mostly composed of smaller diameter roots), were significantly reduced by high temperature stress as noted above.

3.3. Cross-sectional microscopy

The High temperature treatment significantly increased the cortex with epidermis area by 41%; while increasing cross-sectional and pith areas numerically by 13% and 8%, respectively (Table 2; Fig. 2a–b). High temperature stress greatly reduced individual areas of vascular bundle, xylem, fibre bundle and single fibre cell, but did not show a consistent effect on phloem area and secondary phloem with cambium area. The primary phloem with fewer large bast fibre bundles and thinner cell wall under the high temperature stress were found, in comparison with the CK treatment (Fig. S6b, d, g and h). Furthermore, the aborted primary phloem and smaller primary xylem were both evidenced in high temperature treatment (Fig. S6g). Conspicuously thickened secondary xylem was found in the CK compared to that in the high temperature treatment (Fig. S6f and i). Genotypes showed significant differences in all of these anatomical parameters (Table 2; Fig. 2; Fig. S2). In general, genotype Invigor5440 was characterized with a large cross-sectional area, cortex with epidermis circle, pith,

vascular bundle area, xylem rings, phloem area, and secondary phloem with cambium area, while genotype Pioneer45A65 exhibited enlarged fibre bundle and single fibre cell areas as well as an increased total number of fibre cells.

3.4. Stem lodging resistance and its related mechanical traits

High temperature stress did not show a significant effect on S_s and SF_s , although it decreased S_s by 7% and SF_s by 9%, numerically, averaged across the genotypes (Fig. 3). High temperature significantly reduced EI and E by 30% and 43%, respectively; while increased I value by 30% (Table 3). There were significant differences in S_s , M_s , SF_s , EI, and I among the four genotypes. In general, genotype Invigor5440 had the highest S_s , SF_s , EI and I, but the lowest E regardless of temperature treatments.

3.5. Root lodging resistance and its related mechanical traits

High temperature stress induced a 25% reduction in S_r , and therefore reduced SF_r significantly by 25%; while it did not show any significant effect on M_r (Fig. 3). High temperature significantly decreased S_{r-b} by 33%, and decreased root-soil cone diameter by 13% and τD^3 by 33% (Table 4). High temperature had no consistent effect on S_{r-a} . There was a large difference in S_r , M_r , SF_r , S_{r-b} , root-soil cone diameter and τD^3 among the tested genotypes. In general, genotype Invigor5440 had the highest S_r , SF_r , S_{r-b} , S_{r-a} , root-soil cone diameter, and τD^3 regardless of temperature treatments.

3.6. Comparisons and relationships between some lodging related parameters and morphological traits

Under the CK temperature conditions, SF_s was higher than SF_r , and both were higher than those under high temperature treatment. Root lodging (represented by SF_r) was more predominant than stem lodging (represented by SF_s), especially under the high temperature conditions. This was evidenced by a greater reduction in SF_r (25%), with no significant decline in SF_s under high temperature conditions (Fig. 4).

S_s , SF_s , S_r , and SF_r are four important indicators that can be applied to identify the risks of crop lodging caused by stem and root failure.

Table 2

Means of anatomical parameters of four canola genotypes as affected by temperature treatment.

Temperature	Variety	Cross-section area (mm ²)	Cortex with epidermis area (mm ²)	Pith area (mm ²)	Vascular bundle area (mm ²)	Xylem area (mm ²)	Phloem area (mm ²)	Secondary phloem and cambium area (mm ²)	Fibre bundle area (mm ²)	Single fibre cell area (μm ²)	Total no. of fibre cells (no.)
CK	45A65 [*]	83.2 a	15.6 a	39.1 a	16.2 ab	11.2 ab	5.06 ab	3.07 ab	1.99 a	428 ab	4676 a
	13C220	67.4 b	11.2 b	33.3 b	12.6 b	8.4 b	4.19 ab	2.97 ab	1.22 b	513 a	2475 b
	13C204	70.4 b	10.4 b	35.6 b	15.8 ab	12.0 a	3.78 b	2.61 b	1.17 b	392 b	3101 b
	5440	80.9 a	13.0 ab	39.6 a	19.6 a	14.3 a	5.27 a	3.85 a	1.43 b	435 ab	3381 ab
	Mean	75.5A	12.6 B	36.9A	16.1A	11.5A	4.58A	3.12A	1.45A	442A	3408A
High temperature	45A65	82.0 b	17.3 b	41.1 ab	14.2 b	8.9 b	5.30 a	3.35 b	1.94 a	465 a	4171 a
	13C220	74.7 b	16.5 b	34.7 b	12.0 b	8.2 b	3.79 b	2.72 b	1.07 b	424 a	2492 b
	13C204	81.2 b	16.1 b	38.0 ab	12.6 b	8.8 b	3.79 b	2.68 b	1.11 b	295 b	4080 ab
	5440	103.0 a	21.2 a	44.9 a	19.2 a	13.5 a	5.67 a	4.32 a	1.35 b	417 a	3413 ab
	Mean	85.2A	17.8A	39.7A	14.5A	9.8A	4.64 A	3.27A	1.37A	400A	3539A

Within a column in each temperature treatment, means followed by the same letter are not significantly different according to LSD (0.05) test. Lower-case and upper-case letters indicate comparisons among four genotypes and between two temperature treatments, respectively. ^{*}45A65 indicates genotype Pioneer45A65 and 5440 indicates InVigor5440. CK and high temperature treatment stand for 23.0/17.0 °C (light/dark) and 27.01/24.33 °C, respectively.

Correlation analysis (Fig. 5) showed that S_s was positively correlated with stem diameter, EI and I of basal stem, while SF_s was positively correlated with seed yield and EI ($p \leq 0.01$). Both S_r and SF_r were positively correlated with seed yield, S_{r-b} , S_{r-a} , root-soil cone diameter and τD^3 . These parameters also showed a close correlation with morphological traits of root length, surface area, volume and biomass. It was noted that the correlations of S_r and SF_r with morphological traits of lateral roots were stronger than those of taproots.

Several anatomical characteristics were investigated in order to determine their contributions to stem mechanical parameters and lodging resistance (Fig. S7). The correlation analysis indicated that vascular bundle and xylem made significant and positive contributions to the EI and I ($p \leq 0.01$), and therefore displayed a strong correlation with S_s and S_r ($p \leq 0.01$). Cross-sectional, cortex with epidermis, and pith areas were positively correlated with I, but negatively with E.

4. Discussion

To the best of our knowledge, this study was the first to determine the impact of high temperature stress on lodging resistance and the associated mechanisms in canola plants. High temperature stress significantly reduced S_r by 25%, and therefore decreased SF_r by 25%. High temperature treatment, however, showed an insignificant effect on S_s and SF_s , although these parameters also exhibited a decreasing trend (6% and 9%, respectively). In general, significant decreases in root bending resistance, root-soil cone diameter and seed yield were noted

under the high temperature treatment.

More importantly, by comparing SF_s with SF_r , this study allows the assessment of the likelihood of lodging risk caused by the stems or by roots, and the respective changes by high temperature stress. This comparison method between stem and root lodging has been previously made on wheat (Berry et al., 2003a), teff (van Delden et al., 2010) and rice (Oladokun and Ennos, 2006). In this study, the susceptibility of canola resistance to stem and root lodging was quantified by using the “safety factor” method. We found that canola plants were more prone to anchorage failure than stem buckling, and root lodging risk resulting from anchorage failure would further become critical under increasing temperatures with global warming. This was evidenced by the significantly lower SF_r than the SF_s values among the tested genotypes, and the difference between SF_r and SF_s became more critical under high temperature (Fig. 4). It may imply that root lodging is more prevalent than stem lodging, and root lodging should be targeted as the priority trait in canola breeding for a high productivity crop with a rigid root system, especially under future increasing temperature regimes. Agonomists and farmers should pay more attention to the root lodging problem by using appropriate crop management practices, for example, adopting site-specific optimum planting date (Ma et al., 2016), implementing balanced fertilizer management (Wu and Ma, 2016) and choosing cultivars with a more rigid root system.

High temperature stress decreased SF_r due to a large reduction in S_r (25%), while M_r remained unchanged. S_r can be divided into two components, resistance of roots to bending (S_{r-b}) and resistance of roots

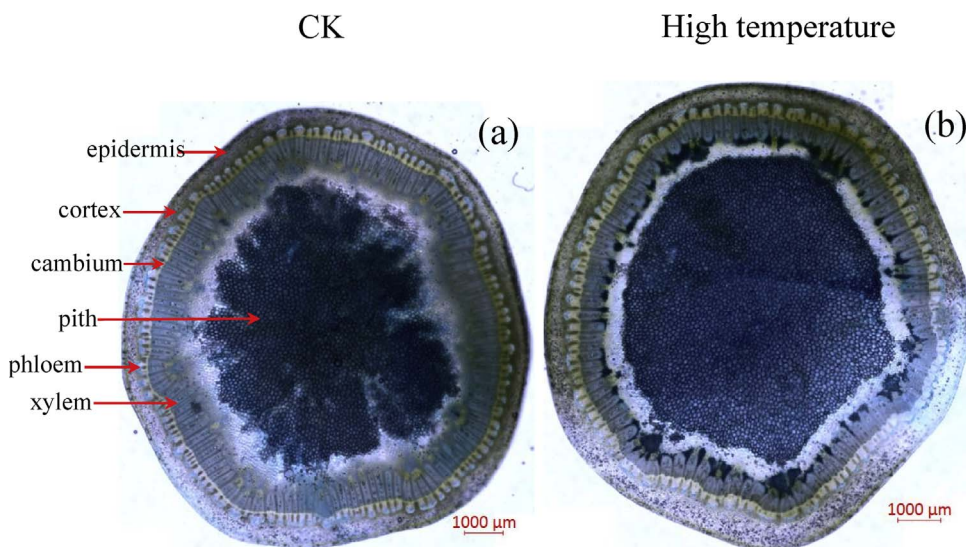


Fig. 2. Cross-sectional image comparison between CK (a) and high temperature (b). CK and high temperature treatment represent 23.0/17.0 °C (light/dark) and 27.01/24.33 °C, respectively.

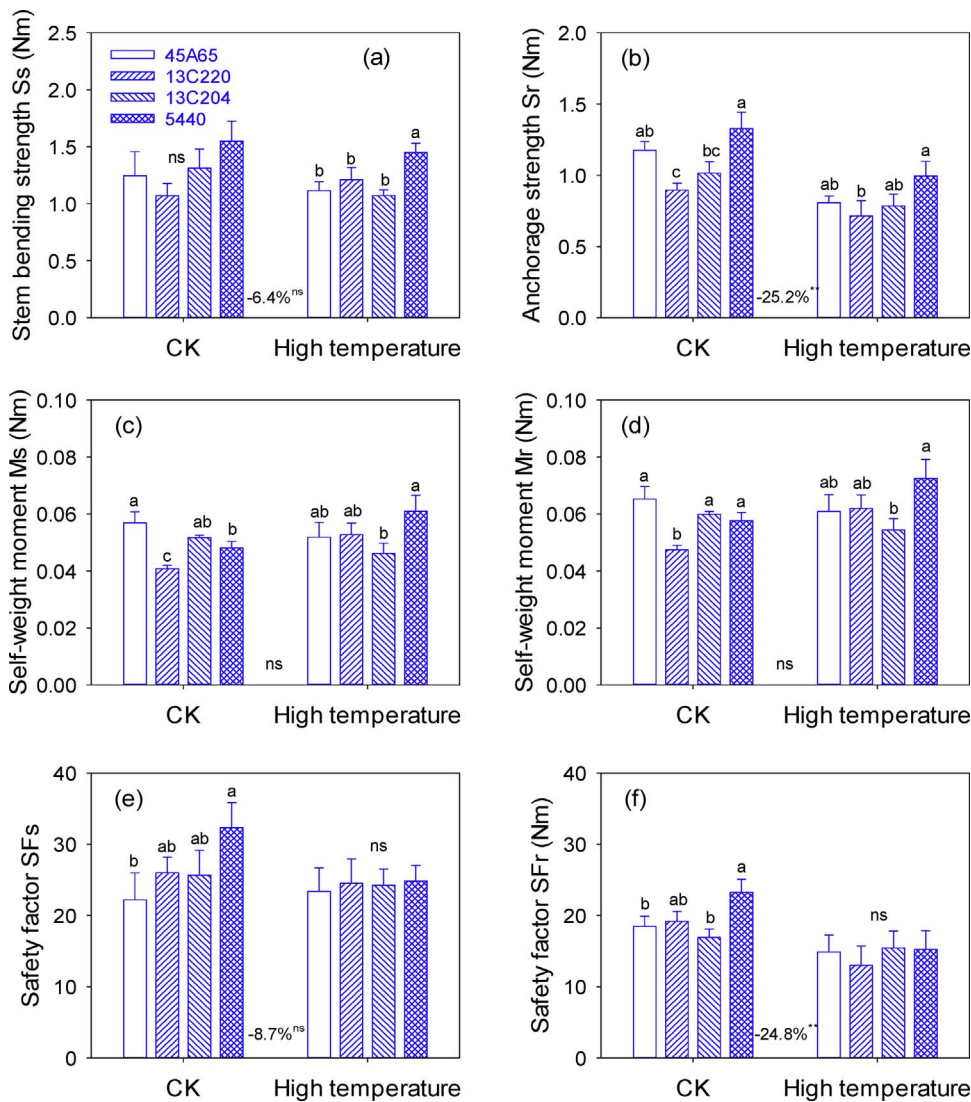


Fig. 3. Means of stem bending strength S_s (a), anchorage strength S_r (b), self-weight moment for stem M_s (c) and for root M_r (d), safety factor for stem SF_s (e) and for root SF_r (f), as affected by temperature treatment and genotype. Bars of genotype means with different letters are significantly different ($p \leq 0.05$). The number between the two temperature groups is the percentage change between high temperature treatment and CK, averaged across genotypes. ns indicates not-significant ($p > 0.05$). * significant at $p \leq 0.05$. CK and high temperature treatment represent 23.0/17.0 °C (light/dark) and 27.01/24.33 °C, respectively.

Table 3

Means of flexural rigidity (EI), second moment of area (I) and Young's modulus (E) of four canola genotypes as affected by temperature treatment.

Temperature	Variety	Flexural rigidity (Nm ²)	Second moment of area (m ⁴)	Young's modulus (Nm ⁻²)
CK	45A65 [*]	0.275 a	212 b	1950 a
	13C220	0.228 a	193 b	1515 a
	13C204	0.238 a	210 b	1605 a
	5440	0.292 a	326 a	1249 a
	Mean	0.258A	235A	1580A
High temperature	45A65	0.179 ab	334 ab	907 a
	13C220	0.185 ab	229 b	1040 a
	13C204	0.143 b	209 b	1030 a
	5440	0.216 a	451 a	628 a
	Mean	0.181 B	306A	901 B

Within a column in each temperature treatment, means followed by the same letter are not significantly different according to LSD (0.05) test. Lower-case and upper-case letters indicate comparisons among four genotypes and between two temperature treatments, respectively. ^{*}45A65 indicates genotype Pioneer45A65 and 5440 indicates InVigor5440. CK and high temperature treatment stand for 23.0/17.0 °C (light/dark) and 27.01/24.33 °C, respectively.

Table 4

Means of resistance of root to bending, resistance of root to axially movement, root-soil cone diameter and τD^3 of four canola genotypes as affected by temperature treatment.

Temperature	Variety	Resistance of root to bending (Nm)	Resistance of root to axially movement (Nm)	Root-soil cone diameter (cm)	τD^3 (Nm)
CK	45A65 [*]	0.710 ab	0.574 ab	4.59 ab	1.31 ab
	13C220	0.562 b	0.446 bc	4.34 b	1.11 b
	13C204	0.620 ab	0.348 c	4.32 b	1.12 b
	5440	0.791 a	0.660 a	4.83 a	1.53 a
	Mean	0.671A	0.507A	4.52A	1.27A
High temperature	45A65	0.359 b	0.410 a	3.73 a	0.72 a
	13C220	0.437 ab	0.417 a	4.05 a	0.94 a
	13C204	0.397 b	0.443 a	3.94 a	0.85 a
	5440	0.599 a	0.366 a	3.94 a	0.89 a
	Mean	0.448 B	0.409A	3.92 B	0.85 B

Within a column in each temperature treatment, means followed by the same letter are not significantly different according to LSD (0.05) test. Lower-case and upper-case letters indicate comparisons among four genotypes and between two temperature treatments, respectively. ^{*}45A65 indicates genotype Pioneer45A65 and 5440 indicates InVigor5440. CK and high temperature treatment stand for 23.0/17.0 °C (light/dark) and 27.01/24.33 °C, respectively. τ and D are the soil shear strength and root cone diameter, respectively.

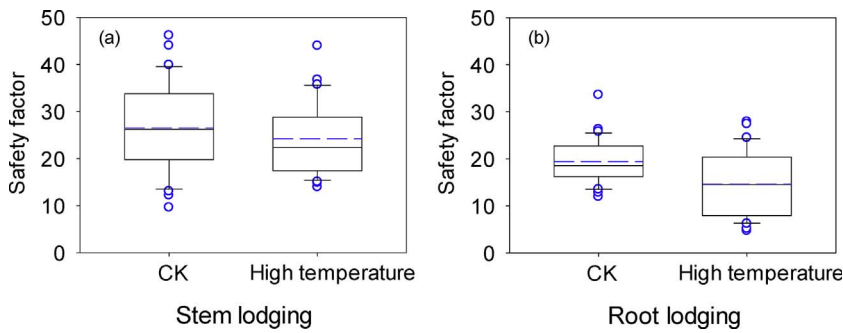


Fig. 4. Susceptibility comparisons between stem lodging and root lodging under CK (a) and high temperature (b) conditions. CK and high temperature treatment represent 23.0/17.0 °C (light/dark) and 27.01/24.33 °C, respectively.

to axially movement (S_{r-a}), according to the engineering mechanics theory (Ennos, 1991). Clearly, our data showed that high temperature stress significantly decreased S_{r-b} , instead of S_{r-a} . In addition, high temperature also decreased root–soil cone diameter (13%) and therefore led to a dramatic reduction in τD^3 (33%). All this evidence illustrated the path to a weaker root anchorage under high temperature stress conditions.

It could be interesting to know how high temperature stress reduces S_r through influencing root development and root structure. In this study, the whole root system was categorized into taproots and lateral roots. There was a greater suppression in lateral roots but less impact on taproots in high temperature than in the normal temperature treatment. The contribution of lateral roots (at windward side) to S_r should be seriously considered, since lateral roots (within diameter class of 0–1 mm) made up the most components of the whole root system (Fig. S5). Lateral roots were grown at the base of the stem and pointed radially outwards and tapered downwards in the current study (Fig. S1). Some lateral roots originated from the taproots also branched to produce tertiary roots with larger angles and spreading out from the

vertical position. An inverted crown shape was formed, as shown in Fig. S1a, similar to those found in rice and wheat, as reported by Oladokun and Ennos (2006). Accordingly, we hypothesized that if a taproot system is well anchored by multiple lateral roots, a greater elliptical root–soil cone volume and thereby greater resisting rotational forces could be retained (Crook and Ennos, 1993, 1994; Berry et al., 2004). This study illustrated that high temperature led to smaller root–soil cone diameter and τD^3 through suppressing lateral root growth, which is in support of our hypothesis. Collectively, these results imply that lower S_r under high temperature conditions compared with the CK treatment was mainly due to the failure of lateral roots. The closer relationship of S_r and SF_r with morphological traits of the lateral roots than of taproots provided further evidence in supporting our hypothesis (Fig. S7). From a field study, we also observed that late-planted canola plants had a simple taproot structure without large lateral roots attached, which was most likely the reason for the smaller S_r (Wu and Ma, 2016).

High temperature did not significantly alter stem lodging resistance in canola plants because the changes in M_s and S_s were both negligible.

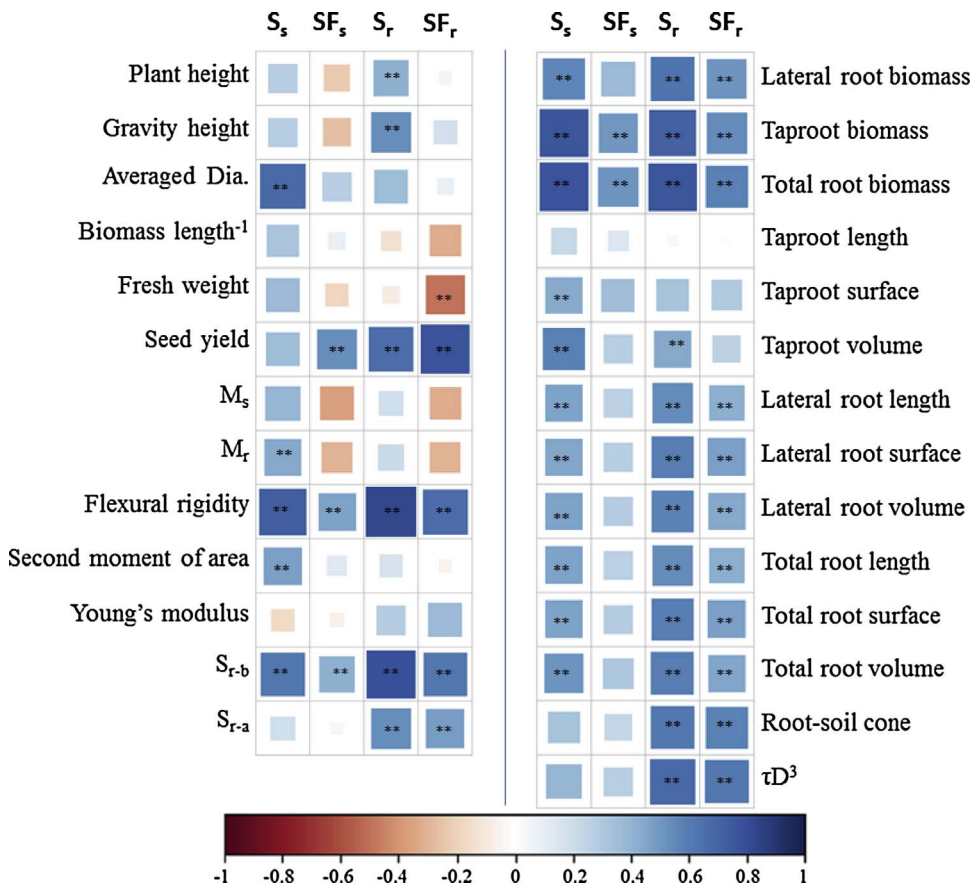


Fig. 5. Significance (colour map) of correlation coefficients between four important lodging-related parameters (S_s , S_r , SF_s , and SF_r), plant morphological traits, mechanical characteristics, and root morphological parameters. ** Significant at $p \leq 0.01$. S_s and S_r refer to stem bending strength and root anchorage strength, respectively; SF_s and SF_r refer to safety factor against stem buckling and anchorage failure, respectively; M_s and M_r refer to self-weight moment for shoot and total plant, respectively; M_{r-a} and M_{r-b} refer to the resistance of the root to bending and to axially movement through the soil media, respectively. τ and D refer to the soil shear strength and root cone diameter, respectively.

The unchanged M_s can be explained by the gravity height and plant fresh weight (Table 1). The unchanged S_s could be explained by two different aspects. In high temperature treatment, assimilates and nutrients that would normally be translocated to the pods (sink) were accumulated in the stem due to sink limitation (Ma and Herath, 2016). As a result, greater stem diameter, dry weight per internode length and second moment of basal stem area were formed. These morphological traits are generally believed to be positively correlated with S_s . In another aspect, the stem EI was largely reduced (by 30%) due to great decrease of E under the high temperature, both of which contributed to a smaller S_s . Thus, these two opposite influencing factors made an offset contribution against S_s . The anatomical data was further in support of this explanation. Under the high temperature treatment, a large area of cross section and cortex with epidermis and pith was a clear indication of increased stem diameter, dry weight and second moment of area. However, the xylem, vascular bundle and single fibre cell areas (that generally believed to strengthen the stem rigidity) were reduced under the high temperature conditions. We also observed fewer larger bast fibre bundles, thinner fibre walls, or even abortion of the primary phloem accompanying with smaller primary xylem in high temperature treatment, in comparison with the CK (Fig. 2; Fig. S6). These data further suggested that high temperature would potentially reduce the stem EI and E , as discussed above.

The negative effect of high temperature on canola growth and seed yield has previously been reported (Morrison and Stewart, 2000; Ma and Herath, 2016). In this study, we observed that high temperature resulted in a higher number of pollen abortions and set fewer pods/seeds with shortened grain filling duration. As a result, seed yield was much lower in high temperature treatment than in the CK (Table 1). In fact, photosynthetic ability at early growth and flowering stage was not suppressed significantly under the high temperature compared to the CK (data not shown). Yield loss was therefore, mainly caused by sink restrictions rather than source limitations, i.e. assimilates from leaf photosynthesis could not be transferred to the pods (sink) and thus accumulated in shoots, leading to much smaller harvest index (Ma and Herath, 2016). Together this has resulted in an increased cortex area of basal stem that served for assimilates storage, such as starch accumulation in the stem under high temperature conditions, which was further confirmed by the anatomical data (Table 2; Fig. 2). Similarly, a disrupting translocation/allocation of biomass between aboveground and belowground section was also noted (Fig. 1 and Table 1). It is argued that assimilates that are likely enabled to be transferred to belowground to support root growth and root function were further restricted by high temperature stress, and therefore stored in the shoots. Wang et al. (2016) suggested that biomass allocation in a tundra ecosystem is projected to shift towards aboveground, rather than belowground plant parts under rising temperature scenarios. Poorter et al. (2012b) also implied that relative high temperature would increase the fraction of stems and leaves and reduce root: shoot biomass ratio, although they suggested that plants are generally more capable of altering organ morphology prior to adjusting allocation between above and belowground biomass. This was consistent with the significant suppression of lateral root growth under high temperature stress conditions in our present study. How this unbalanced biomass allocation between shoots, roots and seeds would change the interspecific allometric relationships in increasing temperature regime with global warming deserves further study.

Breeding genotypes with high lodging resistance is the most efficient way to cope with crop lodging risk (Berry et al., 2003a). Our study showed that canola genotypes differed largely in their overall ability in lodging susceptibility at normal temperature, and lodging resistance was significantly and negatively affected by high temperature stress. This suggests that a large intraspecific variability may exist and could be utilized for selecting for genotypes with improved lodging resistance. The correlation analysis further demonstrated the possibility

to improve stem lodging resistance through selecting for genotypes with a large stem diameter and strong EI, and to increase root lodging resistance by selecting for genotypes with a great root bending force in order to retain strong anchorage strength (Fig. 5). It is worthy to note that modern breeding programs have empirically selected genotypes with more rigid stems (more visible) without compromising plant heights to sustain high aboveground biomass production and great yield potentials. Without paying attention to the root system (because of “out of sight/mind”), this breeding strategy would make stem buckling at a basal internode relatively uncommon in modern genotypes since more biomass is being allocated to the stem rather than to the roots. Instead, this strategy leads to canola plants with greater self-weight moment and weaker anchorage strength that is more susceptible to root lodging (Ennos, 1991; Crook and Ennos, 1993, 1994; Berry et al., 2003a). This situation will worsen under the anticipated rising temperature environment associated with global warming, since our present study suggests that high temperature could result in plants more susceptible to root lodging than to stem lodging. Therefore, breeding selection for a more rigid root system should be targeted as a priority to increase lodging resistance.

Nevertheless, stem lodging cannot be underestimated, because both stem lodging and root lodging may occur at suitable circumstances (Baker et al., 1998). Further breeding program targets for higher yields, which posts a huge implication and requirement for strong support structures of stem base, not only anchorage system (Baker et al., 2014). In addition, improving stem lodging such as increasing stem EI can reduce the inclination angle from the vertical stand and then restrict the self-weight bending moment for the whole plants, which may be beneficial to root lodging resistance.

In this study, the safety factor did not consider the forces generated by wind, rain, storm, or additional weight of wet foliage or the interactions between the foliage and adjacent plants that may provide a degree of protection against lodging (van Delden et al., 2010; Berry et al., 2003b; Baker et al., 2014). It is admitted that this method has some shortcomings, as relative to the modeling approach of Baker et al. (1998, 2014) or the more sophisticated model of Berry et al. (2003b), in which wind loading and related aerodynamics are considered. Nevertheless, the safety factor is regarded as a useful method for comparing the mechanical properties of a plant to withstand physical damage, as suggested from multiple studies (Crook and Ennos, 1993, 1994; Oladokun and Ennos, 2006; van Delden et al., 2010).

In addition, as a controlled pot experiment, the present study has some limitations as compared with field experiments. First, the small pots generally restrict plant growth, especially for root elongation, due to the limited quantity of soil medium and other resources (Poorter et al., 2012a). Second, the temperature of the soil medium was approximately the same as the air temperature, with an approximate 1 °C difference between those in the pot trial. However, soil temperature in canola field conditions could be up to 6 °C lower than air temperature at midday during the flowering stage. Therefore, high soil temperatures under our present growth chamber conditions could have a larger impact on root growth than under field experimental conditions. Third, wider plant density in controlled growth conditions than under field conditions would provide enough space and light for individual plants to grow, and may relieve the interactions between the foliage and adjacent plants. Therefore, it should be noted that these possible drawbacks in small pot experiments compared to field conditions may have some exaggerated influence of high temperature on the growth and development of canola plants. On a positive aspect, water, nutrient, wind and other environmental factors can be better controlled in the growth chamber study than in the field situations, and therefore the impact of high temperature stress on lodging resistance can be clearly separated from other factors. Nevertheless, none of those limiting factors would exert a known impact on the key factors in both of the engineering mechanics theory and safety factor methods to assess crop lodging.

5. Conclusions

This study clearly demonstrated that root lodging resistance was reduced significantly under high temperature conditions, with dramatic reductions in both S_r and SF_r . High temperature stress suppressed lateral root growth, and reduced root bending resistance, root–soil cone dimension, and its shear strength significantly. High temperature stress showed an inconsistent effect on stem lodging resistance, which is in agreement with the engineering mechanics theory and was supported by the anatomical observations. Canola plants were more prone to anchorage failure than stem buckling, and root lodging resulting from anchorage failure would become further prominent and critical under increasing temperature scenario with global warming. This study implied that enhancing root lodging should be advocated as a priority to increase lodging resistance through selecting for more rigid root system. The correlation analysis further demonstrated the possibility to increase stem lodging resistance by selecting for genotypes with large stem diameter and strong EI, and to improve root lodging resistance through selection of genotypes with great root bending force to enhance anchorage strength.

Acknowledgments

This study was financially supported, in part, by the Agriculture and Agri-Food Canada (AAFC) Growing Forward II Canola/Flax Cluster project J-000349.001.01 through the Collaborative Research and Development Agreement between AAFC and the Canola Council of Canada (CCC). We gratefully acknowledge the excellent assistance of Lynne Evenson, and Scott Patterson of AAFC for their technical laboratory work. Lucy Ma, a chartered professional accountant with a Master degree from the University of Waterloo, and Ulrica McKim, a professional soil chemist of AAFC with a M.Sc. from McGill University, have proofread the latest version. AAFC-ORDC contribution No. 17-053.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agrformet.2017.09.017>.

References

- Baker, C.J., Berry, P.M., Spink, J.H., Sylvester-Bradley, R., Griffin, J.M., Scott, R.K., Clare, R.W., 1998. A method for the assessment of the risk of wheat lodging. *J. Theor. Biol.* 194, 587–603.
- Baker, C.J., Sterling, M., Berry, P., 2014. A generalised model of crop lodging. *J. Theor. Biol.* 363, 1–12.
- Battisti, D.S., Rosamond, L.N., 2009. Historical warnings of future food insecurity with unprecedented seasonal heat. *Science* 323, 240–244.
- Berry, P.M., Spink, J.H., Gay, A.P., Craigon, J., 2003a. A comparison of root and stem lodging risks among winter wheat cultivar. *J. Agric. Sci.* 141, 191–202.
- Berry, P.M., Sterling, M., Baker, C.J., Spink, J., Sparkes, D.L., 2003b. A calibrated model of wheat lodging compared with field measurements. *Agric. For. Meteorol.* 119, 167–180.
- Berry, P.M., Sterling, M., Spink, J.H., Baker, C.J., Sylvester-Bradley, R., Monney, S.J., Tams, A.R., Ennos, A.R., Donald, L.S., 2004. Understanding and reducing lodging in cereals. *Adv. Agron.* 84, 217–271.
- Crook, M.J., Ennos, A.R., 1993. The mechanics of root lodging in winter wheat, *Triticum aestivum* L. *J. Exp. Bot.* 44, 1219–1224.
- Crook, M.J., Ennos, A.R., 1994. Stem and root characteristics associated with lodging resistance in four winter wheat cultivars. *J. Agric. Sci.* 123, 167–174.
- Crook, M.J., Ennos, A.R., Sellers, E.K., 1994. Structural development of the shoot and root systems of two winter wheat cultivars, *Triticum aestivum* L. *J. Exp. Bot.* 45, 857–863.
- Ennos, A.R., 1991. The mechanics of anchorage in wheat *Triticum aestivum* L.: II. Anchorage of mature wheat against lodging. *J. Exp. Bot.* 42, 1607–1613.
- Ennos, A.R., 2004. The mechanics of root anchorage. *Adv. Bot. Res.* 33, 133–157.
- Foulkes, M.J., Slafer, G.A., Davies, W.J., Berry, P.M., Sylvester-Bradley, R., Martre, P., Calderini, D.F., Griffiths, S., Reynolds, M.P., 2011. Raising yield potential of wheat. III. Optimizing partitioning to grain while maintaining lodging resistance. *J. Exp. Bot.* 62, 469–486.
- Goodman, A.M., Crook, M.J., Ennos, A.R., 2001. Anchorage mechanics of the tap root system of winter-sown oilseed rape (*Brassica napus* L.). *Ann. Bot.* 87, 397–404.
- IPCC, 2007. Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, UK, Cambridge, pp. 589–662.
- Lobell, D.B., Schlenker, W., Costa-Roberts, J., 2011. Climate trends and global crop production since 1980. *Science* 333, 616–620.
- Ma, B.L., Herath, A., 2016. Timing and rates of nitrogen fertilizer application on seed yield: quality and nitrogen-use efficiency of canola. *Crop Pasture Sci.* 67, 167–180.
- Ma, B.L., Zheng, Z.M., 2016. Relationship between plant nitrogen and phosphorus accumulations in a canola crop as affected by nitrogen management under ample phosphorus supply conditions. *Can. J. Plant Sci.* 96, 853–866.
- Ma, B.L., Wu, T.Y., Tremblay, N., Deen, W., Morrison, M.J., McLaughlin, N.B., Gregorich, E.G., Stewart, G., 2010. Nitrous oxide fluxes from corn fields: on-farm assessment of the amount and timing of nitrogen fertilizer. *Global Change Biol.* 16, 156–170.
- Ma, B.L., Biswas, D.K., Zhou, Q.P., Ren, C.Z., 2012. Comparisons between cultivars of wheat, covered and hullless oats: Effects of N fertilization on growth and yield. *Can. J. Plant Sci.* 92, 1213–1222.
- Ma, B.L., Zhao, H., Zheng, Z.M., Caldwell, C.D., Mills, A., Vanasse, A., Earl, H., Scott, P., Smith, D.L., 2016. Optimizing seeding dates and rates for canola production in the humid eastern Canadian agroecosystems. *Agron. J.* 108, 1869–1879.
- Morrison, M.J., Stewart, D.W., 2000. Heat stress during flowering in summer *Brassica*. *Crop Sci.* 42, 797–803.
- Oladokun, M.A.O., Ennos, A.R., 2006. Structural development and stability of rice *Oryza sativa* L. var. Nerica 1. *J. Exp. Bot.* 57, 3123–3130.
- Peng, S.B., Huang, J.L., Sheehy, J.E., Laza, R.C., Visperas, R.M., Zhong, X., Centeno, G.S., Khush, G.S., Cassman, K.G., 2004. Rice yield decline with higher night temperature from global warming. *Proc. Natl. Acad. Sci. U. S. A.* 101, 9971–9975.
- Pinthus, M.J., 1973. Lodging in wheat, barley and oats: the phenomenon: its causes and preventive measures. *Adv. Agron.* 25, 210–263.
- Poorter, H., Böhler, J., van Dusschoten, D., Climent, J., Postma, J.A., 2012a. Pot size matters: a meta-analysis of the effects of rooting volume on plant growth. *Funct. Plant Biol.* 39, 839–850.
- Poorter, H., Niklas, K.J., Reich, P.B., Oleksyn, J., Poot, P., Mommer, L., 2012b. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytol.* 193, 30–50.
- R Core Team, 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria <http://www.R-project.org/>.
- Ristic, Z., Cass, D.D., 1991. Leaf anatomy of *Zea mays* L. in response to water shortage and high temperature: a comparison of drought-resistant and drought-sensitive lines. *Bot. Gazette* 152, 173–185.
- SAS Institute, Inc, 2008. SAS/Stat Users' Guide. Version 9.2. SAS Institute, Cary, NC.
- Shah, F., Huang, J., Cui, K., Nie, L., Shah, T., Chen, C., Wang, K., 2011. Impact of high-temperature stress on rice plant and its traits related to tolerance. *J. Agric. Sci.* 149, 545–556.
- Singh, R.P., Prasad, P.V., Reddy, K.R., 2013. Impacts of changing climate and climate variability on seed production and seed industry. *Adv. Agron.* 118, 49–110.
- Sposaro, M.M., Chimenti, C.A., Hall, A.J., 2008. Root lodging in sunflower. Variations in anchorage strength across genotypes soil types, crop population densities and crop developmental stages. *Field Crops Res.* 106, 179–186.
- Tao, F., Zhang, Z., 2011. Impacts of climate change as a function of global mean temperature: maize productivity and water use in China. *Clim. Change* 105, 409–432.
- Tripathi, A., Tripathi, D.K., Chauhan, D.K., Kumar, N., Singh, G.S., 2016. Paradigms of climate change impacts on some major food sources of the world: a review on current knowledge and future prospects. *Agric. Ecosyst. Environ.* 216, 356–373.
- Trueba, F.J., van Spronsen, E.A., Traas, J., Woldringh, C.L., 1982. Effects of temperature on the size and shape of *Escherichia coli* cells. *Arch. Microbiol.* 131, 235–240.
- van Delden, S.H., Vos, J., Ennos, A.R., Stomph, T.J., 2010. Analysing lodging of the panicle bearing cereal teff (*Eragrostis tef*). *New Phytol.* 186, 696–707.
- Wang, P., Heijmans, M.M., Mommer, L., van Ruijven, J., Maximov, T.C., Berendse, F., 2016. Belowground plant biomass allocation in tundra ecosystems and its relationship with temperature. *Environ. Res. Lett.* 6, 055003.
- Wu, W., Ma, B.L., 2016. A new method for assessing plant lodging and the impact of management options on lodging in canola crop production. *Sci. Rep.* 6, 31890. <http://dx.doi.org/10.1038/srep31890>.
- Wu, W., Huang, J., Cui, K., Nie, L., Wang, Q., Yang, F., Shah, F., Yao, F., Peng, S., 2012. Sheath blight reduces stem breaking resistance and increases lodging susceptibility of rice plants. *Field Crops Res.* 128, 101–108.
- Wu, W., Duncan, R., Ma, B.L., 2017. Quantification of canola root morphological traits under heat and drought stresses with electrical measurements. *Plant Soil* 415, 229–244.
- Zhu, C., Ziska, L.H., Sakai, H., Zhu, J., Hasegawa, T., 2013. Vulnerability of lodging risk to elevated CO₂ and increased soil temperature differs between rice cultivars. *Eur. J. Agron.* 46, 20–24.